THE HABITS, INSTINCTS, AND MENTAL POWERS OF SPIDERS, GENERA, ARGIOPE AND EPEIRA.

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INTRODUCTION.

> Il n'est peut-être pas d'Arthropodes, qui meritent, plus que les arraignées, d'attirer l'attention du naturaliste, par leur forme, leur industrie, leurs maneuvres. Buffon (His. Nat., p. 172). Wagner (67).

The web of the Orb-weaving Spiders has long been one of the classical examples of animal instinct. It is so definite and complex, and yet so frail a structure and must be rebuilt so often under varying conditions that, *à priori*, we should expect it to furnish one of the best of fields for the study of the variation of instinct. If the cell of the Honey-bee varies so that, according to Prof. Wilder (73, pp. 654,655), who quotes Prof. Wyman in this connection, there may be a gain or loss of one cell in ten, then from a knowledge of the differing conditions under which the spider works, together with the frailty of the web as compared with the cell, we have as much, and even more, ground for thinking that even greater variation will be found here.

The Spider is proverbially a solitary animal. There are social spiders but they are not to be found outside the tropics. Is the study of the spider to open up the rich mine of individu-

ality and adaptation which Dr. and Mrs. Peckham's excellent work (47 and 48) has discovered for us in the Solitary Wasp? Is the method of "trial and error" a common one with spiders as Prof. Jennings (28) has shown it to be in his recent epoch-making work for the lower organisms? The importance of such a study for Animal Psychology can be indicated by quoting from Prof. Lloyd Morgan (39, p. 196). He says,—"Nothing has been said in this chapter concerning automatism or control in the higher invertebrates, such as the bee or the ant. Their actions seem to warrant the belief that in them, too, there is—besides a mechanism for automatic co-ordination—a mechanism for control. But at present nothing is known of definite control centres in these organisms supposing such centres to exist. There is here a fruitful field for investigation, if we could only find a satisfactory point of departure." Since the above was written results by Forel (26), Von Buttel-Reepen (74), Wheeler (71), Miss Field (22) and others, have been published, which make it certain that the social insects do have such control. Prof. Forel's work (25, p. 48), goes to show that the corresponding nervous control centres actually exist in ants.

Social insects, however, may profit by the example set by others of their kind. Then, too, the environment at least always contains the other members of the hive or colony. To this extent, then, the environment is much the same for all members of the same colony. But it is different with the solitary wasp or spider. Each individual must meet successfully an environment more or less different from that of every other individual. With the solitary animal there is no loss of individual rights for the good of the whole group, such as both Comstock (10, pp. 633, 634) and Maeterlinck (51) have seen fit to emphasize in the case of the ant and the hive-bee. The differences between the bee and ant queen as recently well pointed out by Dr. Wm. M. Wheeler (72) are quite in point in this connection. With the spider, the solitary animal, *par excellence*, the individual must vary or die. Wagner has well emphasized this instinct to separate in spiders.[1] It is irrevocable that spiders should scatter as soon they are ready to leave the cocoon, and after that cope with their little world individually. The effect of this scattering is far reaching in many of their instinctive activities.

The number of our native species has been given by some as four hundred. Structurally considered they show as great dif-

[1] Wagner, W: L'araignée aquatique (argyroneta aquatica, Cl.). Son industrie et sa vie. Materiaux de psychologie comparée. Bull. Soc. Moscou, 1900, pp. 61-169. This article is in Russian with a summary in French. I am much indebted to M. de Perott for reading the Russian portion of the article to me.

ferentiation and as high development as many of the insects with which they were classed by earlier zoölogists. From the standpoint of complexity and nicety of development of instinct they are no less deserving of study.

Certainly there is no animal more repulsive to the average person than the spider. This repulsion gives way to one of attraction the moment we get some glimpse of the real life of the animal. Very few, if any of our spiders, are poisonous, the almost universal belief to the contrary notwithstanding. They are not venomous or rapacious as the popular accounts would lead us to believe. The female spiders in ensnaring, poisoning, and feeding upon insects, and even in killing the male spider, may be described as rapacious only by the human observer's too intense subjectivity. They are getting their food by the only method which their evolution has left for their use. One is well within the truth when he says that of all the animals of like organization and habits the mental life of spiders has received far too little attention in a scientific way. In the following paragraphs there will be found a brief survey of previous studies, or such of them as are of interest chiefly from a psychological point of view. There is no other animal about which more has been written that is inaccessible, at least, to the general reader in English.

HISTORICAL ORIENTATION.

For a brief account of the work done prior to 1843 the reader is referred to Menge (37, pp. 2-10). This author's history begins with Aristotle and mentions some twenty-seven other writers, the most important of which are Lister (1678) who, according to McCook, is the father of English Arachnology, Homberg (1707), Leeuwenhoek (1722), Clerc (1757), de Geer (1752-78), Walcknaer (1802-05-06-08-37), whose works give accurate descriptions of genera and species, Kirby and Spence (1823), Herold (1824), Oken (1835), Hahn (1830 and 1831), and Koch (1839). These works are largely systematic and given to a description of structure with many observations of value on the manner in which the web is built, how spiders make use of the thread to bridge across chasms, their food, and differences between the sexes.

The use by spiders of nests or geometrical webs to ensnare prey very early excited the interest of observers in the facts just mentioned. Menge himself has sections on food, the manner of spinning the web by the different genera, the sexual instincts, and with this the nest-building and the care of the young, in which he says the female spider of some species shows a love for the young which even surpasses that found in birds. Here we get an example of the anthropomorphism

which has colored the observations of nearly all of the earlier writers on this subject, and is not yet extinct. Lastly, there is a discussion of sense-perception, the spider as a weather prophet, and the benefits and injuries to be derived from spiders. In his section on sense-perception Menge gives a description of the anatomy of the eye but says that this sense organ has the most marked development of any in the spiders. The active spiders can see an object a few feet distant. They draw back when one approaches to within three or four feet of their web, especially if they have been previously disturbed. The Garden Spider (*Epeira diademata*) has weak vision and allows herself to be touched before moving. It is doubtful if Menge eliminated jars in his observations just recorded. As to the hearing of spiders he takes a negative position and explains their reaction to music by means of the effect of sound waves on their webs. Their sense of taste is weak but not absent. Disagreeable odors seem not to affect them at all as they do us. The sense of touch in the feet must be very highly developed. He seems to have taken special pains to determine how far spiders were reliable weather prophets. His conclusion is a negative one.

Following Menge there seems to have been little published for some years. Blackwall (4) devoted the whole of his three volumes, except the introduction, to a systematic description. Stavely (64) has also written on the habits of British spiders.

Wilder (73) describes the web of the Triangle Spider and as stated above finds, not in this species, but in his additional observations on Orb-weavers, evidence of considerable variation. Hentz (27) during the first half of the last century wrote many articles on the Spiders of the United States. He may well be called the pioneer in American Arachnology. His efforts were almost wholly directed to systematic description with occasional reference to things psychological, *e. g.*, that vision in one of the *Atti* is acute but not unerring.

Dahl (11-14) has published many articles on the structure of spiders, chiefly with reference to their sense powers. Two of these deal primarily with the mental life of spiders. He tested their sense of taste and smell by holding in front of them, or by actually touching them with a glass rod dipped in turpentine, oil of cloves, or ammonia. He concludes from their responses that they both taste and smell. *E. patagiata* Cl., particularly, perceives odors, discriminates different ones, and these have different affective values for her which are not what they have for us. It will be well at this point to call the attention of the reader to Dahl's manifest anthropomorphism. He believes that there are auditory hairs on various parts of the body, principally on the anterior part, which are the organs

of hearing. From the results of tests with flies, bees and pieces of paper fastened to a small wire, he places the limit of clear vision at 2 cm. At this distance some, *Attus arcuatus* Cl., for example, are able to distinguish a bee from a fly. These spiders are able, however, to detect the presence of moving objects at a distance of 20 cm. The color-sense was tested by feeding insects of different colors as well as flies painted with different colors. Two species gave little or no results while two others showed signs of distinguishing the colors. The tactile sense is well developed particularly on the feet and palpi.

In his second article Dahl discusses, (a) Instinct and Cognition; (b) The Social Impulse; (c) The Æsthetic Impulse. He notes that in web-making the spider puts in certain sub-supports when they are needed; also other variations for which external conditions and the properties of the various bodily structures of the spider do not sufficiently account. Therefore these instinctive acts are more or less conscious. He goes yet further in concluding that when, as he finds by actual experiments, *Attus arcuatus* Cl. avoids a certain insect, because she has experienced a few times before, that this kind of insect was covered with turpentine, she is able to and does infer from analogy. He likewise reaches the same conclusion when this and other species avoid beetles and bees after having been fed on these a few times. He thinks that these spiders could have had no experience with this kind of food prior to his tests with them. In some cases he succeeded in inducing them to take flies immediately after they had refused the bee or beetle. He states that their memory for this harmful food lasts at most only a few hours.

Cambridge (8), Campbell (9) and Rainbow (53) are writers on spider habits and instincts from England and Australia. The last named warned against making the web of classificatory value, particularly those spun in confinement. He believes with Wagner (see below) that there may be "fluctuations and variations" of instincts.

M. Eugene Simon (62) has devoted but few pages to spider anatomy and the remainder of two large volumes to a systematic treatment. His programme calls for a third part on Biology such as McCook (see below) has proposed for American Spiders; also a fourth on their Geographical Distribution. He believes that such is the best programme to follow since there are probably many pitfalls in the way of one who knows little or nothing of the anatomy or natural relations of these animals.

Turner (66) noted variations in the webs of a certain Gallery spider. These he considers due to intelligent adaptation; but such is hardly in agreement with the best writers on the subject.

Kennel (32) has made careful observations on the methods by which spiders bridge across chasms or lay down the foundation lines for their webs. He denies that they throw the thread out with such force as to carry it the required distance or that the wind pulls it out. He states that it is fed out with the hind claws. The air currents depending on their strength and direction determining in part the point of attachment of such a thread.

The work of Dr. and Mrs. Peckham stands perhaps as the most extensive and thoroughly reliable from a psychological point of view. In their work on the Mental Powers of Spiders (41 and 42) they have made carefully controlled tests and observations on the senses of smell, hearing, sight, the color-sense, the so-called instinct of "feigning death," the maternal emotions, and the mistakes of spiders. The sense of smell was tested by holding a glass rod with its end dipped in oil or perfume in front of the spider. Each test was at once checked by holding a clean rod in the same position. Many tests were made with different spiders and the authors worked separately. Their conclusions are that only three species fail to respond to the test. It was evident by their various movements that the scent was perceived by all the others.

The sense of hearing was first tested by making loud noises, shouting, clapping the hands, etc. To these there was very little, if any, response. They then experimented with vibrating tuning-forks as Boys (6, p. 149) had previously done. After many tests made with forks of different vibration rate and checked by bringing the non-vibrating fork into the same position, they conclude with Boys that spiders hear. They get some responses after removing the palpi and parts of the foreleg. Yet they do not agree with Plateau (40, p. 384) that palps are useless organs. According to them the end-organs for hearing are not well localized. However, it is not certain that jars have been eliminated and their failure to elicit any response in active spiders points to the fact that the web takes up the vibrations and the spiders feel these.

However, Pocock (50, p. 63), contrary to McCook and the view just stated, thinks that spiders hear and that the tuning-fork experiments have been tried in a sufficiently variable manner to constitute satisfactory proof. I have made no test with the tuning-fork, but have failed to get responses to loud noises.

Some spiders, notably *Cyclosa conica* and *Epeira strix*, responded to the vibrating fork by suddenly dropping from the web. After many experiments they failed to get this response after each test. With a single *E. strix* with which they worked for more than a month there was an increase in this power of

control, thus giving evidence of a short memory. This failure to show the so-called "feigning" instinct is regarded by the authors as rather remarkable, as it is undoubtedly an instinctive reaction of great value to the animal.

These same authors conclude from seeing the males in search of the females and the females for their cocoons that the range of vision for the active spiders may be as great as some eight or ten inches. This is much greater than Forel (24) has put it. Their tests on the color-sense were made by noting, under duly controlled conditions, which compartments surrounded by red, green, blue, or yellow glass the spiders preferred to stay in. They also tested the color-sense in males by painting the females and observing the different reactions of the males, the female without paint having first been placed before the several males; also by separating the female from her eggs and nests and surrounding these with pink, blue, or red paper. The female seemed to become accustomed to finding her nest framed in blue and wanted to return there even if the blue had been changed in place and pink then surrounded the nest and eggs. From all these experiments the authors infer that spiders see colors and the first series indicated a preference for red "much more marked than that found by Sir John Lubbock for ants, and the spiders had not so positive dislike for blue."

Various alarming stimuli were given to spiders by these authors in order that they might observe the so-called "feigning" instinct. This reaction consists simply in dropping from the web or nest and lying with legs flexed as if dead. Their findings from more than two hundred experiments on nineteen different genera may be indicated as follows (41, pp. 416-417): "Out of the species with which we experimented we found one which would endure a moderate amount of pricking with a needle, and a second which did not move when its legs were pinched. Beyond this there was no stoicism under anything that approached bad treatment, although a few species allowed themselves to be handled without showing signs of life. We do not believe that any spider which came under our observation ever fell into a Kataplectic condition. . . . There is no need to call in 'Kataplexy' to explain the origin and development of a habit which can be easily explained by natural selection alone." Robertson's (54) conclusions agree with the above. He holds that for active spiders the stimulus producing the "sham-death" reflex must be sharp and sudden. With the sluggish the reflex posture is more continuous and practically independent of the nature of the stimulus. In the active the reflex may be carried out by the thoracic ganglia alone, or even by the ganglia of the two posterior or anterior segments. In the sluggish it cannot be induced without the head-ganglia.

The "sham-death" in intact spiders is a complete tetanus. With the supra and sub-œsophageal ganglia removed the reaction is carried out but is weaker, in at least one of the active species; it has a longer latent period and it is a rhythmically interrupted tetanus. This reflex is probably a means of escape in emergency, and "conscious volition" can have nothing to do with it unless consciousness can be an attribute of each thoracic ganglia.

The Peckhams also found that those spiders which carry their cocoon about with them will take up a pith-ball or a web-covered shot instead. But when allowed the choice between a pith-ball and their cocoon they take the latter in preference, provided they come into contact with the cocoon. This proves that, since these spiders carry their cocoon underneath their body, they are unable to recognize it by sight alone. Tactual stimuli must be present for an effective perception. They also infer that the muscular sense in these spiders is poorly developed since they persist with much difficulty in carrying about the heavy shot. But the instinct in which this act finds its setting is necessarily so strong and important for the preservation of the species that we should be slow to make such an inference. However, this species was not an Orb-weaver, and need not have so finely developed a muscular sense.

These same authors have published three different articles (43 and 44) on Courtship in spiders of the family *Attidae*. They describe and give drawings of the antics of the males and in the last article discuss the bearings of their results on the Darwinian and Wallacian theories of selection. They maintain that their observations uphold the theory of sexual selection as stated by Darwin.

McCook (35 and 36) in his many articles published by the Philadelphia Academy of Science and his three large volumes "American Spiders and their Spinning Work," treats their natural history with special regard to their industry and habits. Of special interest to us in the present paper is the fact that he counts and measures a few webs of some species and finds evidence of considerable variation. He also brings together the previously known results in their appropriate places. His large works are popularly written, and although he is anthropromorphic in statement, he is somewhat loath to grant intelligence to those spiders he has most studied.

Prof. Emerton in his two excellent books (19-20) and many earlier articles deals with the structure and habits of spiders common to the United States and often notes as well the variation in the number of parts of the web, together with interesting observations on the sexual instincts, etc.

Wagner (67 and 68) is certainly one of the most careful

writers on spider habits and intelligence. His mental attitude toward spider activity reminds one strongly of that of Bethe toward ants and bees. They are looked upon pretty much as "reflex-machines." As suggested above he finds variations in instinctive activity. These are great enough to furnish a foothold for natural selection. He gives a few observations which support his view that such variations have their origin in the germ-plasm. He is certainly right in explaining many of the adaptations as instinctive. But in denying all intelligent power to spiders he is perhaps taking an untenable position.

Prof. Montgomery (38) with much painstaking and careful observation has described the mating habits of many of our common spiders. Very few of the orb-weavers were included in his list. He considers that the approach to the female by the male is a very interesting field from a psychological point of view. He holds that the courtship of the male is more remarkable since he must re-charge the palps with sperm. To this he has given name of *sperm induction*. He concludes that the male is guided by tactual and visual stimuli in his search for the female and that the strongest male wins. The female exercises no conscious choice in her selection of the male.

Lécaillon (34) describes the nesting habits of one species which lives inside her nest with the young. This author tests the strength of the maternal instinct by separating the proper mother from her young and noting her attempts to replace a foster mother. He finds the maternal instinct strong and that it lasts for some seven or eight days.

Miss Pritchett (52), in addition to giving a good bibliography and a review of the work already done on the senses of hearing and smell, obtained, by careful tests with a tuning-fork and other methods, a negative result for hearing in the two species tried. She thus confirmed the results obtained by the Peckhams for active spiders. Irritant and non-irritant oils were used in the tests on smell. Both males and females responded to both these even when the palps, hairs on the legs, or the first pair of legs respectively, were removed. Hence the end-organ for the perception of odors must be distributed more or less over the whole body.

Methods of Study.

The species chiefly dealt with in the present paper are: *Argiope transversa*, *Argiope riparia*, the Shamrock Spider—*Epeira trifolium*, the House Spiders—*Epeira Sclopetaria*, *Epeira strix* and *Epeira patagiata*. The results of some observations on a few other species will also be given. For description of most, if not all of the species herein mentioned, the reader is referred to Professor Emerton's work (20) whose nomenclature I have used throughout.

The first problem selected for solution was the determination by actual count and otherwise of the range of variation between webs made by different members of the same species as well as between successive webs of the same individual. In order to do this most conveniently it was thought best to bring as many spiders as possible into the laboratory. If this was done, they must be given water to drink (since it has long been observed that they naturally take a good deal of water), various insects for food, and suitable places to build their webs. The plant-stalks bearing the nests or to serve as main supports for the webs were usually placed in bottles containing water and these placed on tables or wide window-sills. Other stalks were placed near so that the spider might find at hand as nearly as possible the same conditions as she would have had on the outside. Each spider was numbered and, since many different rooms were used, some very large, the spiders were correctly traced in most cases when they wandered, as they often did, from their assigned places. As there is great variation in size and markings between the individuals of the same species that may be brought in at any one time, they were the more easily followed. During the first season's work almost every spider observed was killed and preserved in alcohol. These were later submitted to Professor Emerton for identification.

For some of the *A. transversa* (this species not having a nest but, while not at work standing in the centre of the web,) boxes and old aquaria frames with removable glass sides and top were used. However, these were soon discarded for the reason that they often led to the building of an abnormal web. the spider bending the upper half almost at right angles with the lower if the top of the case was in the way. Toward the close of my work in late autumn the spiders and the surrounding grass were well sprinkled with water from an atomizer. This is a necessary precaution if these animals are to be kept normal.

Photographs of many of the webs were taken and drawings from some of these will be given. All these drawings are, therefore, very accurate, the lines in the negatives being very carefully followed in each case. It is especially difficult to get good photographs of webs unless one uses Emerton's method of sprinkling them with a solution of shellac in alcohol. This I could not do as it would probably have made the conditions surrounding the spiders altogether too abnormal.

From what has been said it will be seen that the various habits and instinctive activities, indicated at the beginning of this paper, were open to observation and study, both in the field and the laboratory. Many observations on *riparia*, especially on the mating habits, were made during the last season

near Hoopeston, Illinois. It should be clearly kept in mind that two brief seasons are too short a time in which to gather data which will support conclusive generalizations. It has, nevertheless, seemed worth while to publish the data gathered together with the tentative conclusions which they suggest.

Choice of the Place for a Web, the Nest and Material for the Nest.

In the pseudo-scientific literature the statement is often found that spiders exercise great intelligence in choosing the place for the web. The different sorts of places chosen by the same individual are many, and it is well to look into the matter more closely before believing (Büchner 7a, 80, p. 315) "that spiders know just where to place their web in order that most insects may be ensnared by it. Practice, experience and reflexion must also guide the spider in the important choice of the locality in which it shall spin its web, in order to catch the largest amount of prey. Before all it likes those places where the rays of the sun and dancing midges may be united with the possibility of a hidden retreat for itself, or where a slight draught blows flying insects into the outspread nest, or where fruit attracts them."

Indeed, if such were the case we might well say, that the spider shows the highest degree of intelligence. But while practice and experience may be worth something, my observations of web building have inclined me to accept Wagner's (67) explanation as nearer the truth. The determining factors are, (1) The place where the particular species concerned habitually lives or hunts, (2) The shape of the foundation of the future nest, and, (3) The peculiarities of the spider's organism. As is evident from the form of statement Wagner speaks primarily of the nests of spiders and not of their webs. We fail to see in the above any room for any psychic factors other than those which may be called instinctive. In placing the web imitation of the old by the young is impossible. None of the young of the species here considered ever see the old, and if they did their range of acute vision is too limited to allow them to profit by the example of the old. Apparently the young from the first choose the place for their web in the same way as the old. To be sure, they must be governed somewhat by their own size for upon this the size of the web in a measure depends. But the latter is also determined by the place chosen. This is in accordance with the third factor mentioned above. Again, although spiders wander some, the large sluggish kind here considered do not go far. For example, a space of low land near a brook not more than thirty feet square had at one time 17 *E. trifolium*, 12 *A. transversa*, 2 *A. riparia*,

2 *E. strix*, 2 *E. corticaria*, besides a large number of more active kinds. The second factor, the shape of the foundation of the future nest applies as well to the web. It is, in fact, the most important of all. Concrete examples will illustrate this as well as the others. *A. transversa*, No. 106, was brought in and placed in the same bunch of grass in which she had spun her webs in the field. This was done by digging up enough earth to hold the grass roots in place. This was placed in a small aquarium frame so that the grass stems might be the better supported. There were no glass sides or top. Her first attempt was to build from the end of the frame to the top of the table. In this case a line from *a* to *b* in Fig. 1 would have been the top horizontal foundation line of her web. Her first web spun in-doors was in the grass as shown in Fig. 1. This lay in a plane at right angles to that which the first would have had. She began this web only after more than an hour of wandering about. Fig. 2 shows her third attempt and second web. This, as may be seen, is in as different a position from the second as this was from the first. Fig 3, shows her third web, much smaller and higher up than the preceding. Here she spun several webs and then the last one from the side of the frame to the top of the table. The degeneration in the successive webs I am certain is due largely to the fact that she found less and less firm supports, and smaller space in which to hang her web. In the first two attempts described above, where I saw her choose the place for her web, her method was clearly one of try and re-try, in the first having almost laid down the third line to the web and yet giving up for that day. *E. trifolium*, No. 48, was seen to persist for some time in an attempt to lay down the fourth foundation line in such a way as would have enabled her to make a web of the typical form and size. Failing in this she seemed to make the most of the possibilities.

The place for and the material out of which to make the nest which *E. trifolium* and the House Spiders use would seem to be chosen in exactly the same manner. The former will bend over one or more heads of grass, Fig. 4; she may, and usually does, use leaves or blossoms of golden-rod, the leaves of birch or of some weed. *E. strix*, *corticaria* and *angulata* usually select leaves which they also bend into a bell-shaped nest. Yet *E. strix* may use the blossom of Yarrow with no silk lining at all, the leaves of ironweed, or pull together into a bunch some heads of fine grass. She even occupies the abandoned nest of *E. trifolium*. Any of them may make use of any corner, or crevice, which will furnish them with the thygmotactic stimuli over the surface of the body which seem to make them feel more at home. This would mean that they

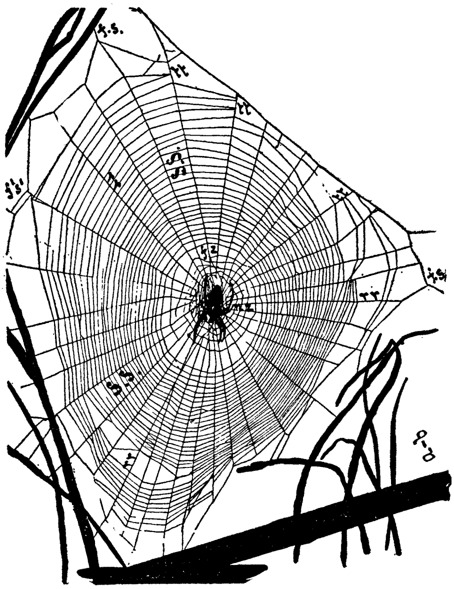

FIG. 1.

Fig. 1 represents the first web spun indoors by *Argiope transversa*, No. 106. It, like all the figures in this article except 6 and 7, is a drawing by Dr. M. T. Thompson from photographs made by the author. *f. s* = foundation zone; *rr* = radii: *ss* = the main outer spiral space; *f.z.* = the free zone; *n.z.* = the inner zone; *tt* = the turnings about; *f.' s.'* = extra sub-supports, and *a—b* represents the top horizontal line of the first web which No. 106 attempted to build.

are positively thygmotactic during the day. When night comes, they move out and stand in the centre of the web. Though *E. trifolium* habitually stays in the nest during the day except when wrapping prey, I have had three under observation which, on finding no convenient place for a nest, stood in the centre of the web *à la Argiope*, detected the presence of prey, and wrapped it in a perfectly normal manner. Though the nest is normally 30°-40° from the vertical and above the centre, Fig. 4, it is not always so. It may be below the centre or to one side. This is yet another indication that its location may be a secondary consideration.

It is evident from the facts just given that the species here considered use for the nest whatever place and material comes most conveniently to hand. Their instinct must allow them a wide range of selection. Intelligent choice of either is apparently out of the question. Wagner (68) states that the water spider (*Argyroneta aquatica*) shows no selection of water plants. They are always those gathered together by the elastic threads which she, like all spiders, always spins as she

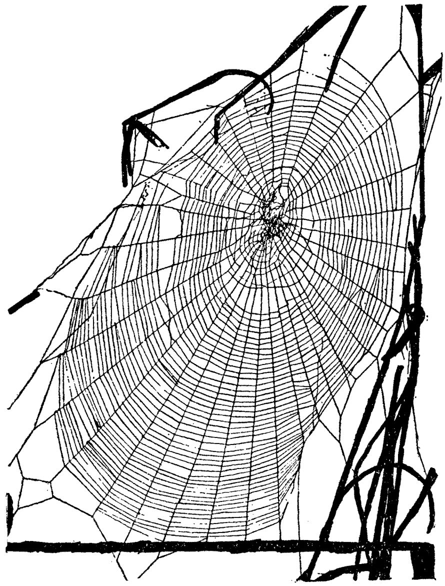

FIG. 2.
The second web made by No. 106 in-doors. Note the difference from the first, Fig. 1.

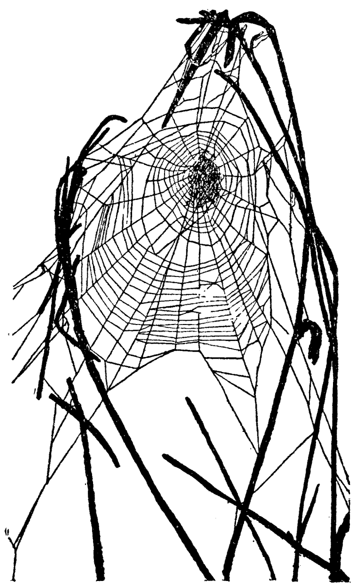

FIG. 3.
The third web made by No. 106 in-doors. The effect of change of place is marked.

wanders round. She, like the spiders above, may build in a plant, in a depression in a piece of rotten wood, or in an empty shell. Such was his explanation of McCook's observations on the Turret Spider which was found to have made use of the cotton, used by the collector to close an opening in the lower part of the spider's turret, for a part of its underground dwelling.

The Manner of Building the Web and its Variations.

The preceding section has led us naturally to wonder if the spider shows a like adaptation in the actual making of the web. As is clearly evident from what has been said of early writers on spider habits, the manner in which spiders build their webs has been fairly well known for a century or more. Therefore, the aim here will be more to emphasize the variations to be found, giving only such other facts as are necessary to furnish a sufficient setting for those in which we are primarily interested.

Before proceeding with the variations to be found in web building, it will be well to fix upon some of the terms used in the description of the web. I shall use, so far as possible, the nomenclature of McCook (35, I, p. 54). That part of the web marked *f. s.*, Fig. 1, is the foundation zone where are placed the foundation lines, usually stronger than the other lines. The radii, *rr*, are the lines radiating from the centre. The spiral space, *ss*, is that of the main outer spiral. The space, *f. z.*, is the free zone. The inner zone is indicated by *n. z.* over which the spider is standing.

The spider's first task is to lay down the foundation lines of the web. She may be able to walk completely round the place in which she has chosen to place her web. If so, she holds the thread away with one hind claw from the objects on which she is walking, pulls it taut, fastens it at the corners, and she has the sides of her web. These may be three or more. If she must bridge over a chasm, she does so by feeding out a loose thread from her spinnerets with her hind claws until it strikes some object. In the semi-darkness in which I watched my spiders I learned to expect that the spider would make a start directly if she began to move the hind feet in this feeding-out manner. Her tactual sense is so acute that she detects the moment the thread strikes, at once draws it taut and travels along it. Some writers have claimed that the spider allowed the wind to pull out this thread, she only starting it; others have thought that the spider threw it out with force enough to carry it the required distance and attach it to some object. But Kennel's (32) observations are in favor of the method first stated, and I have seen *transversa* repeatedly feed out the

thread. The distances bridged are too great—being sometimes 30-40 feet,—to be explained by either of the other methods. It will be seen that by this means the spider may travel from place to place through the air as well as make supports for her web. The spider varies from one method to the other supposedly because of the character of the objects on which she builds. In case webs are hung to horizontal threads bridging wide spaces, these threads are doubled and redoubled until they are remarkably strong.

In making the web the main supports are the first to be put in. Kirby and Spence (33 a, p. 232) suggest that some species may put in some of the radii first. A single observation of *E. sclopetaria* would point to the same as being true of this species. Then the spider lets herself down from about the middle of the horizontal support at the top and thus forms the first of the radii. After this the radii are put in from the centre, the spider walking along an old ray and holding the one just being spun out with one foot so that it will not touch and adhere to the one she is walking on. After fastening it to one of the side supports she walks back along it and perhaps doubles it as she returns. The order in which she puts in the rays is not without interest. The general plan is to alternate from above to below the centre and from left to right, though this order is not a rigid one. Some have said that the spider has no appearance of measuring on the supports in order to see where to fasten the radii. My observation is that she does have such an appearance. Spider No. 106 saw fit to cut some of the lower radii which as first put in would have thrown the lower part of her web much out of line, Fig. 1. She did this by cutting them at the outer ends and swinging down on them until she struck the grass below. This made the entire web lie more nearly in the same plane. After the radii were all in No. 106 proceeded to test them. Her manner of doing this was to face in turn each group of radii and pull sharply several times after which she strengthened some of them. Above and below the centre in Fig. 1 may be seen three or four radii which are unusually strong. This, as well as the number of radii, indicate that the spider in building her web balances one side against the other. In the above example the grass supports were probably somewhat less stable than is usually true of those used by spiders in their natural habitat. Yet, judging from the finished product, cases not unlike this happen on the outside as well. No. 106 found that at one time she needed a sub-support, *f.' s.'*, Fig. 1, and stopped to put this in, taking up the interrupted work again at the right place. Her next step was to put in the spiral from the centre out, Fig. 4. This serves her for a guide when she later begins, usually at the

lower outer edge, to put in the sticky spirals. The guide lines are cut out as they are reached by the spider when she is putting in the sticky parallel lines. As she places these latter we see that now if ever the spider needs all of her eight claws. One cannot but believe that here there is need of the nicest correlation of tactile and muscular sensations together with the most delicately co-ordinated muscular contractions. It is a revelation to see an *E. angulata* in almost total darkness fasttening these outer spirals to the radii at the rate of almost one per second. In fact spiders are said by most writers to spin as perfectly in the dark as in the light. They must, therefore, be guided largely, if not wholly, by tactile and motor cues. There can be no doubt that here the spider measures, one claw always marking the place where the spiral is clamped to the ray by the spinnerets. All my observations would indicate that in putting in these outer spirals the spider goes round in a direction contrary to the hands of a watch having put in the guide lines in the opposite direction.

Before quite reaching the centre the spider ceases to put in outer spirals and to cut out the guide lines which here are very near each other. This space without spirals is the free zone, *f. z.*, Fig. 1. It is left so, according to McCook (35, I, p. 58), in order that the spider may easily pass from one side of the web to the other. The few cases I have seen would indicate that the spider may perform this act very quickly.

After the parallel lines are all in the *Argiope* spread the spinnerets and plaster or darn the centre with wide strands of web. As they have no nest and habitually stand in the centre of the web this gives strength to the web and also a shield to stand behind, Fig. 6. However, this darning of the centre is often omitted. The *Epeirae* do not plaster over the centre but gnaw out the fuzz collected there in drawing taut the radii, etc., Fig. 5. Fig. 4 shows a failure to do this. But before the *Argiope* take their position in the centre, they go directly below and turning round to pass upward, spread the spinnerets, throw the abdomen from side to side, and make the zigzag or "winding stair," Fig. 6. There is also an upper half to this structure. Yet, as is shown in several of the figures, the whole or a part of this is frequently absent, the upper half more often. Male spiders of *A. riparia* have sometimes the faintest suggestion of a zigzag.

The function of this part, according to McCook, is to strengthen the web. May it not be also to aid these silver, black, and yellow spiders as they stand astride of the zigzag to a better mimicry of the plants about them, and thus be neither conspicuous marks for birds nor apparently different from objects which insect prey alights upon? However, it is so incon-

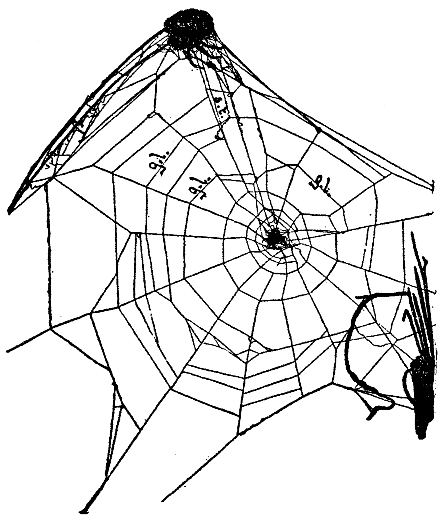

FIG. 4.

Fig. 4 represents a half-finished web of *Epeira trifolium* showing the guide lines, *g. l.*, also the failure to gnaw out the fuzz in the center.

FIG. 5.

This and Fig. 4 show the imperfect nest this spider often makes, as well as her usual position with one fore-claw on the signal thread, *s. t.*

stant that its value, whatever it may be, is at present somewhat questionable.

Many of the webs of *Argiope* have what are called side-screens or guards. One such is shown in Fig. 9. These serve for protection and to cause insects to fall into the web. They would seem to be absent whenever there are no suitable objects near by to which to fasten the threads. They have been absent in whole or part from most of the webs I have seen.

Another adaptation not always required is to tie back the grass in order to make a place for the web. This is done by *E. trifolium* as well as by the *Argiope*.

The webs of all spiders here considered have a normal slant of about 30° from the vertical. This slant is of much service to the spider. The web catches falling objects as well as flying ones. A more important consideration, however, is that when the insect is cut out it swings free from the web, hangs to the spinnerets and hind claw of the spider, and can be more easily carried up to the centre or to the nest. They have an awkward time of it if, as I have seen, they attempt to carry the insect on the upper side of the web. The webs vary within the widest limits as regards slant. That the slant given to the web is of the hit and miss sort with the constant corrective of the general instinctive tendency toward the normal position, is evident from what was said above of No. 106. No. 23 of the same species spun a series of some 10-12 webs in the same branched twig and no two had the same slant.

The repair of webs by spiders has furnished material for much discussion. This seems to follow the same method as the building of the web as a whole. My spiders appear to illustrate again what Wagner has pointed out for nests of his water spiders. He purposely injured the nest to see what the spider would do. Their method of repair was like the making of an entire nest. Where the spider would be expected to use her intelligence she does not. In repairing the web *Argiope* may put in the repair at a different slant, suggesting that she is proceeding by her method of building an entirely new web. Often one sees webs of *Argiope* with two zigzags, Fig. 6. This shows how stereotyped is the connection between different acts of the web-spinning process. The two zigzags indicate that the spider in making the new web felt compelled to complete a new zigzag though she had not cut out the old one. This cutting away of the old web is the point at which Prof. Emerton thinks the spider offers us one of her very best examples of intelligence. When she comes to the last act, the making of the zigzag, which now she need not do, a second one is put in, and, as shown in Fig. 6, it often does not coincide with the first. These two zigzags are often found in *A. riparia* webs in a

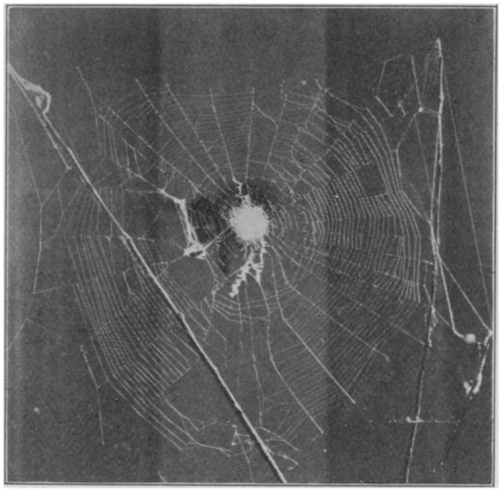

FIG. 6.

A photograph of No. 23, *Argiope transversa*. This shows the quick adaptation of which this spider is capable, (See page 337.) Note the double zigzag and re-darned centre behind which the spider is standing; also the wide strand which the spider spun as she chased the fly over the web; the wrapped fly and the strand with which she anchored it to the centre. She has two feet on this anchor thread.

state of nature. If the animal were exercising intelligent control would she do this? Again, the act just preceding the making of the zigzag, that of "darning" the centre, as I have called it, is gone through with in the same way until the centre is so well "darned" that the spider on the other side is hardly visible, Fig. 6. The fixed sequence of tactual or muscular impressions (or both), which guides the spider in making the web at first, probably impels her to go through all the remaining parts of the process.

The young of spiders are said by some to build imperfectly, but both Blackwall and Wagner deny this, Romanes (55, pp. 216, 217). The webs of the young are small but very perfect. I refer especially to the young of *E. sclopetaria*. I have seen many of these spinning their webs in torn places of the web of a larger spider. They work as rapidly as the old, and the finished web is as perfect. Indeed, according to my own observations and, as I have seen stated elsewhere, their webs may be more perfect than those of the old. This might well be from the fact that the sticky lines of the web are not pressed together by their slight weight, and the web being so small (often no larger than a half-dollar), it is not so dfficult to find a suitable niche for it.

There are thus many adaptations to particular circumstances to be seen in the above examples, which I believe are fairly typical. Many spiders, no doubt, find weak supports for their webs, as must have been the case with No. 106. There can be little doubt that, since spiders of even the same species must build where the surroundings are widely different, they must have this instinct so plastic in certain particulars that the individual can make much use of the "trial and error" method. This, as will be shown later, need not involve conscious adaptation. Yet where the conditions are such that there can be less change, as gravity for example, and certain directions, after the centre of the web has been once located, the actions are more stereotyped and fulfill in part the requirements of "tropisms."

A Quantitative Measure of the Variability of Instinct as Determined by Counting the Elements in Parts of Webs.

In order to get a more exact measure of the amount of variability in this web-building instinct, counts of five different parts of the Orb-web were made. These were as follows: (1) the number of supports or attachments to objects; (2) the number of radii; (3) the number of outer spirals above the centre; (4) the number of outer spirals below the centre; (5) the number of inner spirals inside the free zone. As many successive webs as possible were obtained from each individual spider. Series for *A. transversa* and *E. trifolium* for both in- and out-of-doors were obtained. With *E. sclopetaria* separate counts were not necessary for the reason that she is equally at home in either place. A few counts were made for different individuals of *E. strix*, *patagiata*, *corticaria* and *A. riparia*. As the latter is very closely allied to *A. transversa*, and my general observations have been perhaps more extended with her than any other, I am certain that what is shown to be true of the *transversa* webs will be found to be true of *riparia* when actual counts are made. "Outside" and "inside" indicate that the webs were spun either in-doors or out-of-doors. Av. stands for the average, M. V. the mean variation, and Ex. V., the extreme variation.

Epeira trifolium.

In field. No. of Spiders.	No. of Webs.		Supports.	Radii.	Outer Spirals. above	below.	Inner spirals.
20	90	Av.	12.15	23.07	14.46	27.02	8.38
		M.V.	1.94	2.28	2.92	3.62	1.11
		Ex.V.	7	13	3	7	4
			19	31	23	37	11

Inside. No. of Spiders.	No. of Webs.		Supports,	Radii.	Outer Spirals. above	below.	Inner spirals.
16	42	Av.	10.28	18.9	9.06	17.88	5.27
		M.V.	2.19	2.79	3.16	4.29	1.09
		Ex.V.	7	12	3	5	3
			24	25	21	32	9

Individual E. trifolium.

	Supports	Radii	Outer above	Outer below	Inner spirals
Inside.	7	20	—	20	5
	7	22	—	20	7
Spider No. 3,	9	23	15	20	8
	13	22	12	19	5
	11	22	15	24	5
Spider No. 12,	10	21	13	24	7
	10	25	13	22	6
	12	23	11	24	4
	10	20	7	5	5
	9	19	14	5	6
Outside.	14	19	11	16	4
Spider No. 160,	12	23	14	26	4
	14	25	16	27	6
	13	21	14	27	6
	14	27	16	30	7
	12	26	16	28	8
	17	16	10	18	5
	11	20	14	26	4
	14	20	11	26	7
	14	23	14	24	4
Spider No. 164,	9	28	17	29	5
	12	22	18	28	6
	12	23	21	34	7
	14	27	19	27	8
	12	26	18	29	6
	14	20	13	26	7
	15	23	21	35	6
	14	26	19	34	7

Argiope transversa.

In field. No. of Spiders.	No. of Webs.		Supports	Radii	Outer above	Outer below	Inner spirals
18	52	Av.	13.71	27	16.16	28.44	8.1
		M.V.	2.54	6.27	1.66	6.09	1.13
		Ex.V.	8	17	3	8	3
			19	44	31	51	15

Inside. No. of Spiders.	No. of Webs.		Supports	Radii	Outer above	Outer below	Inner spirals
8	23	Av.	13.5	26	10.6	22	7.5
		M.V.	2.02	4.78	7.13	7.78	1.69
		Ex.V.	9	15	2	8	5
			18	35	29	38	12

Individual A. transversa.

	Supports	Radii	Outer above	Outer below	Inner spirals
Inside.	17	33	25	33	7
Spider No. 106,	15	35	19	44	11
	12	27	3	18	12
	14	27	4	23	8
	18	22	4	19	9

	Supports.	Radii.	Outer Spirals. above	Outer Spirals. below.	Inner spirals.
Outside. Spider No. 106,	15	20	22	10	9
	13	—	29	14	6
	19	33	37	23	7
Inside. Spider No. 23,	14	33	29	38	10
	9	30	14	30	9
	12	34	22	36	8
	13	32	22	33	10
	15	24	3	10	10
Outside. Spider No. 117,	18	32	18	20	11
	14	20	12	16	9
	12	22	9	11	9
	9	20	11	18	6
	13	19	5	8	5
	10	22	12	17	7
Outside. Spider No. 39,	9	17	5	8	5
	12	19	7	14	—
	12	21	10	14	8
	12	20	11	11	9
	15	22	9	10	8

Epeira Sclopetaria.

No. of Spiders.	No. of Webs.		Supports.	Radii.	Outer above	Outer below	Inner spirals.
33	82	Av.	8.36	18.57	17.13	22.04	4.83
		M.V.	1.12	2.51	3.43	3.94	.86
		Ex.V.	5	11	7	14	3
			14	25	28	35	10

Individual Sclopetaria.

	Supports.	Radii.	Outer above	Outer below	Inner spirals.
Spider No. 92,	7	17	8	14	4
	9	23	22	20	4
	8	20	16	28	—
	7	17	23	24	4
	8	23	28	27	4
	10	23	22	27	6
	8	16	15	14	4
	10	16	10	22	4
	9	15	21	28	4
	9	17	21	28	5
	11	20	24	32	5
	9	18	20	26	4
	10	16	19	23	4

Individual Epeira Strix.

	Supports.	Radii.	Outer above	Outer below	Inner spirals.
Outside. Spider No. 2a,	13	21	19	35	8
	9	21	17	23	5
Spider No. 6a,	10	13	10	13	3
Inside. Spider No. 17,	9	20	28	43	6
	10	23	23	43	7
	10	28	20	29	7
	9	26	25	41	7
	10	22	11	22	6

Individual Epeira corticaria.

	Supports.	Radii.	Outer Spirals. above	below.	Inner spirals.
Outside.					
Spider No. 4a,	16	19	13	25	6
Spider No. 5a,	7	25	18	20	7
	11	26	11	14	7
	11	26	15	18	8
Spider No. 1a,	15	22	22	42	9
	19	22	20	39	11

Individual Epeira patagiata.

Inside.					
Spider No. 51,	8	17	25	33	5
	8	15	22	30	6
	7	16	14	22	5
	7	16	14	22	5
	10	19	21	26	7
	9	20	21	26	5

Individual Argriope riparia.

Outside.					
Spider No. 2 (n. s.),	14	31	21	32	14
	16	26	13	34	—
	17	22	12	23	8
	20	23	8	24	8

In making up the above tables care has been taken to leave out a very few of the most irregular webs made by spiders either in-doors or out-of-doors. Such irregularities were clearly due to very bad weather or to abnormal physiological condition. The most important part of each table is the number of radii. The outer spirals above and below come next in value. The supports and the inner spirals were most difficult to count and are of least value. It is not at all difficult to see from the above tables that there is great variation in the number of parts of the spider's web. The M. V. rarely falls below ten per cent. of the average and much oftener is much larger. The statement often found that "spiders build their webs with almost mathematical precision" needs qualification. To be sure, the members of the same species build a web, at any rate, of *generic*, if not *specific* value, if we make the web our basis of classification. But this value depends on the general arrangement of the parts, the size of threads used, and the presence or absence of certain parts. It could not be determined from the number of parts alone. Rainbow has therefore rightly objected to making the web of taxonomic importance, especially those spun under other than normal conditions. There is too much variation. Changes probably both external and physiological demand, as we have seen in the concrete examples of the building of the web, changes of procedure from the individual. There is greater variation in the results obtained from webs spun in the laboratory than from those spun outside.

But the number of spiders is very different. We do not know but that this difference would be diminished by using a larger number of spiders. Again, on the inside, every bit of the web was usually torn away by me each evening. Outside, the spider did her own tearing down of the old web before building a new one. From what little I have observed of this tearing down the spider in many cases leaves intact the old foundation lines. Combining these conditions with the change from out-of-doors to in-doors the greater variation is not surprising.

The results for individual spiders show that the variation is in part an individual matter. It is due, in large part at least, to particular conditions which the individual in question must meet. That this factor of variability between successive instinctive acts of the same individual appears in all the important tables above is of great significance. This would seem to be a much better measure of variability than the variation found to obtain between a single instinctive act, performed but once by a single individual of the same species, for example, the bending over of a blade of grass to make a cocoon. Prof. Davis (15, p. 47) has proposed such a measure of the variability of instinct. Indeed, he has found such by measuring the length of the fold in the blade of grass which the unknown spider uses for its cocoon. His abstract I quote in full: "A series of 222 nests of another species of spider, which binds grass or sedge blades in a peculiar fashion to form boxes for the protection of its eggs, was exhibited and a preliminary report on the variations and their causes was presented. Marked individual differences, including several anomalous types, appear, which probably represent (apart from accidental variations due to mechanical conditions) both variations in instinct and ingenious 'accommodations' to unusual conditions. Variations in length of the regular 'modal' forms conform closely in their distribution to the normal curve of frequency. In spite of the undoubted presence, in this case, of numerous factors which it is difficult to eliminate, it is thought that an objective measure of the variability of instincts may be possible."

How much of this variation, one would like to ask, is due to the size and age of this unknown spider or the difference in the width and thickness of the blade of grass? That some of the variability shown in the above tables and in other portions of this paper is due in part to similar causes I have no doubt. This will be made clearer by the curves given below. Until we can get, however, successive products of the same instinctive act by the same individual, and prove that such give us variation, there is not much progress to be hoped for in arriving at a satisfactory quantitative measure of the variability of

instinct. At any rate, careful observation of the behavior of the spider in the performance of these instinctive acts is very desirable. This has not yet been done for the making of the cocoon above referred to.

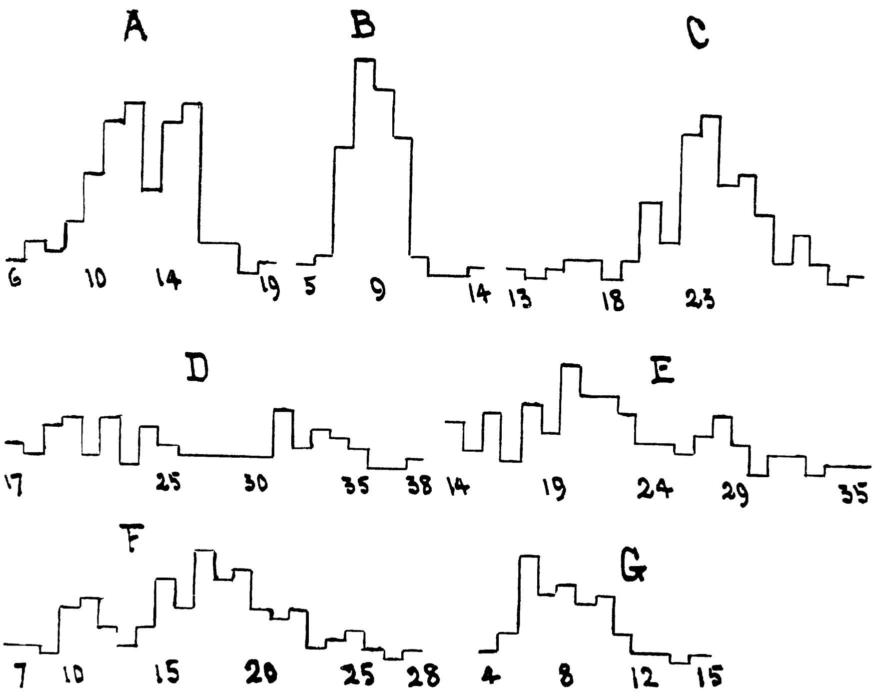

FIG. 7.

A represents the distribution of the number of *supports* in 90 webs of 20 *E. trifolium* spiders in the field; B the same of 82 webs of 33 *E. sclepetaria;* C of the radii of the *E. trifolium* in A; D of the radii of 52 webs of 18 *A. transversa* in the field; E of the Outer Spirals (below) of the *E. sclopetaria* in B; F of the Outer Spirals (above) of the same webs as in E; and G of the distribution of the number of Inner Spirals of the *A. transversa* in D.

In Fig 7, A, B, C, D, E, F, G, will be found a graphic representation of the distribution of the number of elements in the parts of the web by the method of surface frequency. The number of elements is represented on the base line in inches. The number of times this number of parts occurs in the webs is indicated by distances in inches above the base line. Only a few of the diagrams that could be made from my data will be represented here. The terms used in connection with each curve are made intelligible by the preceding tables. The above curves show more clearly than the tables which pre-

cede the great amount of variation to be found in the webs of spiders The supports and inner spirals vary within much narrower limits. If we had cases enough it is possible that these curves would all more closely approximate the curve of normal probability for mental traits. They might not show what some of them seem now to show. For example, in D, representing the radii of *A. transversa* in the field, there are really two curves, that is, the curve which we should expect for an animal that is at the present time developing two separate types of habit in this respect. However, as separate calculation shows, these separate rises in the curve are due to the fact that I have combined two separate counts; one, the first made late in the season, and the second made the next year but much earlier in the season. It is probable, then, that the age and size of the spider, the season, and possibly other factors, make it advisable to control the conditions, if possible, a little more carefully, at least to take cognizance of their presence, in the interpretation of results. However, the curves do not make it impossible that, so far as parts of the web are concerned, new habits might arise. As pointed out on pp. 310, 314, both this variation and, indeed, the possibility of the development by a single species of two types of habit are not totally new suggestions. Emerton (20) in a number of places in his recent book states that the number of radii for certain species varies between given limits. McCook (35, I, p. 107 ff.) also has counted and measured the webs of a number of different species. This same writer also states that certain *E. triaranea* and other species often spin threads across the open sector usually left free by this species. He suggests that here there may be a development into two different types of habit. However, no one (except Prof. Davis, as indicated above,) so far as the writer knows, has undertaken by this or any other means to obtain a quantitative measure of the variability of instinct.

In this connection occurs the very interesting, if at present insoluble, question as to whether function precedes structure in development. The above facts suggest that change of function may lead the way in the development of new structures or species. The nervous system being the most plastic tissue in the body might naturally be expected to lead in those accidental or other changes that give an opportunity for the working of natural selection.

The Time of Spinning the Web and the Stimulus which Sets the Web-spinning Act Going.

It was not long after my counting of the parts of the web began that I was curious to know just when the webs were spun, especially by the *Argiope* and *E. trifolium*. I often

visited these spiders in the laboratory in the evening and first part of the night, but found that they did no more than move about a little. Two *transversas* which were in the field did nothing during the first part of the night. This was not true for *E. sclopetaria* and *angulata*, the young of which spin at most any time of day, while the older ones of these species usually spin at nightfall.

As a result of the above observations I began to watch at three A. M. On the first morning Nos. 106, 105, and 119, all *transversas*, began to move at about the same time. Nos. 98 and 99, *E. sclopetaria*, moved about, although they had spun webs at four P. M. on the day previous. This was at 5.30 A. M. about the middle of October. On the following morning the same reaction to the first appearance of dawn was noted. One 16-candle power incandescent lamp was left burning some twenty feet distant. This may account for the fact that No. 106 began before 5 A. M. on two later occasions.

On. Aug. 17th of last year I visited eleven *A. riparia* in the field at 3.30 A. M., and found all but two with the webs about two-thirds finished. These two had apparently just finished spinning. This was an agreement that I had hardly looked for. Again, in the month of September, I visited other webs at 5.30 A. M. and found one *E. trifolium* and three *A. transversa* with webs not quite finished. Prior to this I had noted that an early morning rain had stopped several *A. riparia* at about the same stage of progress in the making of their webs.

Most of the above facts seem to suggest that a common stimulus which sets them spinning is the amount of light. It is hoped in the future to determine this matter by actual experiment. With *A. transversa* and *A. riparia* this would seem to be when dawn begins to break, with *E. sclopetaria* and *E. angulata* when twilight gives way to darkness or perhaps in the morning as well. I tore away the webs of Nos. 98 and 99 at about the time in the evening for them to build if they were going to do so. They spun the next morning with the *transversas*. At any rate, so far as this study has gone, there seems to be a pretty definite reaction in this regard. Of course, one cannot be absolutely certain that light was the stimulus, but the coincidences point in that direction. Changes in weather and other conditions modify this reaction.

The above agrees well with what Prof. Emerton (20, p. 161) says of the three House *Epeirae* of which *E. sclopetaria* is one. "The webs are made usually at nightfall, very young individuals beginning to spin soon after sunset and larger ones beginning later, those that are full grown often waiting until dark, but some of them will occasionally spin their webs at any time of day."

We must conclude, then, so far as evidence goes, that the change from darkness to light and *vice versa* is the stimulus which usually sets the act of spinning going. The time at which the web is made would seem to have some significance in the life of the spider. I have seen *sclopetaria* remain undisturbed in her nest when her web was filled with flies. She and her close relatives probably feed at night, and hence the making of a fresh web at nightfall. Just what causes some or most of the young of this species to settle upon this time as they grow older, and in how far they do so, is a very interesting point which awaits further study. The *Argiope* and *E. trifolium* probably feed mostly in the daytime and on day-flying insects. Hence the importance of having a fresh sticky web with which to begin the day's work. If made the previous evening the web would be a much less efficient instrument for ensnaring prey.

In this connection may be mentioned the place which the spider is said to hold as a weather prophet. Büchner (7 a, p. 317) says: "When a storm threatens, the spider, which is very economical with its valuable spinning material, spins no web, for it knows that the storm will tear it in pieces and waste its pains, and it also does not mend a web which has been torn. If it is seen spinning or mending, on the other hand, fine weather may generally be reckoned on, so that spiders have long served as weather prophets." However, the observation of the Peckham's (41, p. 383) led them to write as follows: "After having observed spider after spider building a new web on the eve of a storm, how shall we explain the statement (which I have just quoted from Büchner). This would be, no doubt, the wisest way for spiders to act under the circumstances and Dr. Büchner is in very illustrious company when he—unconsciously, of course—orders the actions of such simple creatures in full accord with the higher reason." My observations agree perfectly with those of the writers last quoted. The reader will recall that Menge's conclusion as stated on page 309 is in agreement with this. I have seen any number of webs the making of which was stopped by a storm. Again, I have seen giant *riparia* webs, two and one-half feet across, spoiled by a rain only a short time after they were completed. In late autumn No. 39, *A. transversa*, spun while it was raining and sleeting. Facts such as these make it impossible to believe that these species are good prognosticators of the weather.

THE FEEDING HABITS AND INTELLIGENCE OF SPIDERS.

The feeding habits of spiders have been studied both in-doors and out-of-doors. Insects, grasshoppers, flies and bees were caught and placed on the web. Observations were also made

on the behavior of spiders which caught their own prey in a perfectly natural manner. Notes were made at the time the spiders were feeding. In what follows the emphasis will be placed on the variations found to occur in the several acts which together constitute the feeding habits or instincts rather than on the identities which are, of course, of easy demonstration.

As pointed out above all spiders are voracious eaters. This explains their noticeably rapid growth, as well as the great variation in size in spiders which evidently have come from the same cocoon. Since, as in the case of *A. riparia*, and *transversa*, the young hatch in winter and do not come out of the cocoon till May, it is possible that there is a by no means insignificant struggle for existence while the young are in the cocoon so many months together; and the suggestion of Wilder and Lécaillon that the young eat each other is not at all an impossible one. This would certainly explain the marked differences in degree of development which are found. *E. sclopetaria* that live near a door to a house where there is an abundance of flies may become as large as a full grown *E. trifolium* while others, certainly as old, may be quite small.

The spider's first task is to detect the presence of prey in the web. To do this *A. riparia* and *transversa* stand at all times in the centre of the web on the under side with the eight feet carefully placed on as many radii, these being drawn a little taut by the spider, Fig. 1. *E. trifolium* and the house spiders usually stay in the nest with head pointing downward and with the first or second claw on either side holding a thread which is attached to the centre of the web, Figs. 4 and 5. This thread is spun last as the spider returns to her nest and is free from everything except the centre of the web and the spider's claw. It is a sort of signal thread. The House spiders may place their feet on the ordinary rays. When an insect strikes the web none of these spiders, as a rule, rush headlong after it. The *Argiope* may often be seen to draw the rays just a little tighter. *E. trifolium* and the House spiders start just a little out of the nest. It is as if they needed first to be awakened. They may stop several times before they reach the centre, presumably to see if their own movement has shaken the prey out of the web. At the centre they try, by halting a longer or shorter time, to locate the exact place where the insect may be found. That the centre is a better place for locating prey than any other in the web is shown by the fact that spiders often go the centre when a much shorter way is open to them. Boys (6, p. 149) has shown experimentally with the tuning fork this value of the centre for purposes of orientation. They may also halt after they have left the cen-

tre. It is very interesting to see the spider during one of these halts suddenly jerk on the rays several times and then apparently wait for the stir which this should cause the insect to make. Whether or not the spider is then in an expectant state of attention is at present impossible to determine. Though usually so, spiders are not always infallible in locating their prey. They sometimes go four or five centimeters too far to one side.

The *Argiope* often do not wrap flies until they have carried them back to the centre. They may treat them as they always do a grasshopper—wrap them without first biting and poisoning them. Individuals of *E. trifolium* have always wrapped first except in one case in which I observed No. 170 catch a fly in her mandibles and not wrap until a strong wind apparently compelled her to do so. *E. trifolium*, *E. sclopetaria* and *strix* after wrapping usually carry the insect up into the nest, but there are exceptions to this. Before *E. trifolium* carries the food to the nest she, like the *Argiope*, returns to the centre of the web. Spiders generally spin a thread after them wherever they go, that at any time they may retrace their steps. The *Argiope* are usually anchored to the centre of the web so that they are prepared at once to spin their threads on the sudden appearance of food. These threads are often made much stronger than a single one by a spreading of the spinnerets. But in wrapping the insect this thread connecting them with the centre is lost and a new one must be spun; hence the trip back to the centre. I have seen *E. trifolium* spin as many as three of these threads back to the centre. This is, without question, an adaptation to enable her to care for an extra large insect. Nos. 106 and 105 have returned to the centre two or three times when the insect was an especially difficult one to deal with.

Nos. 14 and 106 showed caution at times in wrapping grasshoppers. Caution was also evident in the actions of No. 24, a very large *trifolium*, when she was trying to get over the web to her food. The single *E. strix* which I had in the laboratory had been fed on flies until one day I gave her a grasshopper. This led to some interesting actions on her part, as there seemed to be an element of surprise in her behavior. Before she reached the centre she stopped to jerk the rays two or three times. At the centre there was a halt for an instant. After leaving the centre to go down she stopped three times, giving to the radii several quick jerks each time. After reaching the grasshopper she tapped it some fifteen or more times before climbing on its back to search for a vulnerable spot. Finding it where spiders often find it, between the abdomen and thorax, she at once began to poison her victim. It does not take long

for this poison to take effect, as the grasshopper ceased to struggle within less than two minutes. The web of *E. strix* is not suited to holding strong insects like a grasshopper, as I have observed out-of-doors. McCook's observation, that she is nocturnal in habits, suggests the same thing. It may be that this was a new food to her; she certainly acted as if it were. I tried feeding her grasshoppers after this, but could never get them ensnared in the web. They always escaped before she reached them.

A. transversa No. 23 seemed to show quick adaptation to a sudden change in circumstances when a blow fly was placed in her web. Just as she was on the point of reaching the fly it suddenly tore loose from the web. In an instant she was after it and had spun at the same time a wide strand behind her, the latter evidently because she was, as it were, already in the act of wrapping the insect. Fig. 6, page 325, shows the path she followed in catching the fly and the wide strand with which she anchored it to the centre. This is, at least, a rather extraordinary occurrence to which the spider did not fail successfully to adapt herself. We might interpret this as proof that the Orb-weaver can become an active and hunting spider, though I am not inclined to make so much out of it. Earlier writers have recorded observations seeming to show that an Orb-weaver losing a number of its legs took on the roving habit and attempted to secure its food in this way. Heineken and others, according to McCook (35, I, p. 78), have thrown considerable doubt on this point by removing, in some cases, all but three of the spider's legs and yet finding no change in the habits. A number of spiders have come under my observation which had suffered the loss of one, two, and even three legs. An example of the last I had under observation for three weeks. She showed no disposition to become a rover, spun a normal web, or fairly so, caught insects as well as a normal spider and received in a hostile manner the attention of a six-legged male. She was certainly hostile enough toward him to have been the cause of his deformity.

No. 14, *A. transversa*, treated some of the flies fed to her in a manner peculiar to herself. The instant she seized the fly in her jaws she let go and swung free, but at once climbed the thread she was suspended by, and was back at the centre where she wrapped her prey. This would do for small prey and was a matter of economy; for this procedure would no doubt save the web from being needlessly torn.

The spider has been said to show intelligence in the treatment of objects that fall into its web. Such, for example, as the cutting out of pieces of rotten wood, large insects, etc. I have tried tossing pieces of the hairy seeded spike of foxtail

grass into the web of *riparia*. She wrapped the first one thrown in but on feeling of it more carefully cut it out, and let it drop, seeming to save as much of the wrapping as possible. After a short interval another piece was tossed in. She did not wrap this but merely cut it out, treating several more in the same way. After a time she paid no attention whatever to the pieces.

Was this an indication that she very readily detected the sham, modified her behavior, and later ignored it altogether? Does this behavior transcend the possibilities of instinct alone? Dahl's experiments, the results of which are given above, led him to conclude that spiders infer from analogy as well as profit by experience; also that they have a memory lasting several hours. But these experiments are almost all identical with Morgan's classical chick experiment and certainly need imply nothing more than ability to profit by experience. In many of my feeding experiments I have found spiders very uncertain quantities. They refuse to act when, to the human observer, there is no assignable reason for such a refusal. My attempts to corroborate Dahl's results (14, p. 173) are, so far, too few to allow of any generalizations. One *E. trifolium* would come no nearer than an inch and a half to the grasshopper which had been dipped in turpentine. The odor must have reached her from this distance, and I concluded that the solution was too strong. The Peckhams (41, pp. 393, 394) also found some evidence of ability to modify the "feigning instinct," and some proof of memory. Montgomery (38, p. 84) thinks that a male spider is just a little more wary in his attention to a second female if he has been treated roughly by the first just a short time before. From the results obtained by these writers and the few of my own which bear upon this point it is probable that spiders can learn and retain for a short time what they have learned. It is certainly premature to conclude that they infer from analogy. Further experiments are a great desideratum, however, in order that we may know how their intelligence compares with that of ants, bees, wasps, and the lower vertebrates.

The Web-Shaking Instinct.

One of the most curious of the reactions to be found in two of the species of spiders dealt with in the present study is the instinct to shake the web. The Peckhams (41, p. 411) have noted something like it with *Epeira strix*. "Number one shook her web with sharp jerks when a branch to which it was attached was moved; and did the same when she was lightly struck." I have seen *Cyclosa turbinata* do this when her web was jarred by near approach to it. In one case only was I

certain that *E. sclopetaria* shook her web. The amplitude of this vibration may be, for the centre of the large webs, at least four or five inches. This is not at all unlike the rhythmic swing which the boys like to give to the long foot-bridges across streams to the consternation of their weaker or more unfortunately placed companions. This is the only case with this species of which I am sure. It is true that this jerking may be analogous only to that which is to be seen in many spiders, when they shake the web, when objects fall into it. They seem to try to dislodge the foreign object by jerking sharply on the rays. And this may not be the same as the slow regular vibration which *riparia* and *transversa* give to their webs. At any rate, this may be brought about by bringing some object into the spider's range of vision which, if she is otherwise undisturbed, seems to be about one-half an inch. Other disturbances may also cause it. The spider may remain in the centre and shake the web or run to an upper corner shaking the web as she goes.

The usefulness of this instinct is not far to seek. Any enemy that is in pursuit over the web is placed in close straits in order to avoid the sticky concentric or parallel threads; or what is better still any large insect, a grasshopper, for example, which has only a partial lodgment and would do the web great harm if allowed to kick undisturbed, is aided in his efforts to escape.

Vision in Spiders.

This section follows immediately that on the instinct of shaking the web because it was the manifestation of this latter that led me to observe and test the sense of sight in spiders. As I have already said, the object, the sight of which is to induce the vibration must be brought very near to the spider. But I soon observed that after the vibration was started the object need not be brought at all so near in order at once to cause the spider to increase the amplitude of the vibration. After this increase subsided another test could be made with the same results. Many tests have been made in this way. At least I am convinced that to awaken the spider, so to speak, with a preliminary disturbance is sufficient to increase her range of vision, at least, some six or eight times. This was for a piece of white card-board one inch square and fastened to the end of a brass wire so that it might be handled conveniently. With *riparia* I have noted that a movement of my body two and one-half feet away was followed by an increase of vibration. Further experimentation is necessary before I can be absolutely certain that jars were entirely eliminated. I have thought that clothes light in color and moving objects were detected when

farther away than darker and fixed objects. Of course, if the spider is tested while she is shaking the web this is equivalent to making the object move.

Another sign which they give on seeing an object consists in elevating slightly the posterior end of the abdomen. The distance which is sufficient to produce this is about one inch. This would seem to be about the normal limit of vision for *E. trifolium* so far as I have been able to test it. One of the latter species failed to see another individual of her own species, which was made to invade her nest, until very near. *Agelena naevia* did not spring for flies until they were about the same distance from her. I have, nevertheless, seen a *Phidippus tripunctatus* jump a distance of fully an inch and a half and catch another spider, *Tetragnatha laboriosa*, which was eating a fly in her own web.

The distance given above for *Argiope*, at which they seem to detect the presence of objects is not by any means unheard of. Hentz and Bingley have both given to spiders a very keen sense of sight. The Peckhams (41, p. 402) on the basis of their observations of both males and females make the following statement: "The ocelli of some spiders, then, enable them to see objects at a distance of at least ten inches." Forel (24), however, calls a fly stupid that could not escape from a spider, but he probably underestimates vision in spiders.

The spiders of the authors just quoted are perhaps the more active or hunting spiders. It is not asserted here that the large and sluggish *Argiope* can do more than detect the presence of an object at a distance of six to ten inches. It would be quite another thing for them to distinguish a fly or another small spider as prey and spring upon it at this distance. But the question may very well be asked: Would it not be rational to suppose that, after being made to vibrate once and thus put on the alert, the spider should be able to see farther and better and thus at any rate detect the mere presence of a large and light colored object? It will be recalled that Dahl gave spiders both a far and near range of vision although their eyes consist of eight of the simple ocelli of insects and have little or no power of accommodation.

It may be, however, that all we have in the above is a proof that attentive vision in spiders is more effective than inattentive vision. As suggested in the section on Feeding Habits, there is some proof that the spider must be first awakened before she starts off to catch and wrap an ensnared insect. These results on vision would indicate all the more that the spider is in a more or less sleepy condition while she is in the nest or standing in the middle of the web. The spider's manner of life is such that we might expect it to require periods of profound

rest. The making of the complex web in from three-quarters of an hour to two hours, as well as the wrapping of prey, demands the expenditure of an extraordinary amount of energy in a comparatively short time. It would seem best, then, to regard the above facts as most satisfactorily explained by greater alertness.

THE MATING INSTINCT IN ARGIOPE.

This instinct is one of the most interesting in spiders, or for that matter in the whole animal kingdom, and this is especially true when the subject is approached from a psychological point of view. Some of the difficult questions that press for answer may be stated as follows: What starts the male in his search for the female and does he search for her at random or is he guided by some sense or senses susceptible to special stimuli? Do males of closely allied species ever get on the webs belonging to other species? Are there definite steps in the male's approach to the female? How far is it true that there is a battle for supremacy among the males? Does the female exercise any choice among the males? These and other questions are suggested in the investigation of this instinct.

In what follows I shall not try to solve any of these, but merely offer a few facts gathered in an incidental way on some of the questions raised. My observations are confined, so far, to two species, *A. transversa* and *riparia*. The male of *riparia* was first observed on the edge of the web, or on the side-screens to the web, of the female. In a few instances the male made a very imperfect web of his own. The next step showed the male above the female at the upper edge of the web, and on the same side. From here he gradually went down toward the female and often stood for hours an inch or so distant. Next the male spent several hours, in one case a day or more, on the opposite side of the web and very close to the female. With the male in any of these positions one could easily see that he was keenly alive to every movement of the female. If the wind shook the web so as to make it necessary for her to readjust herself, the male followed her with a readjustment of his own. Just before she moulted the male again took his position on the same side of the web and immediately above her. See Fig. 8. This moulting takes a variable time with different females. My observations as to the manner of moulting agree perfectly with those of Montgomery (38, p. 145). He says "the moult in all spiders follows the same plan: a horizontal split of the old skin along the side of the abdomen and of the cephalothorax (here just above the leg and the jaws), so that the skin breaks into a dorsal and ventral piece. This is quite different from the process of moult in insects and crustacea." This manner of

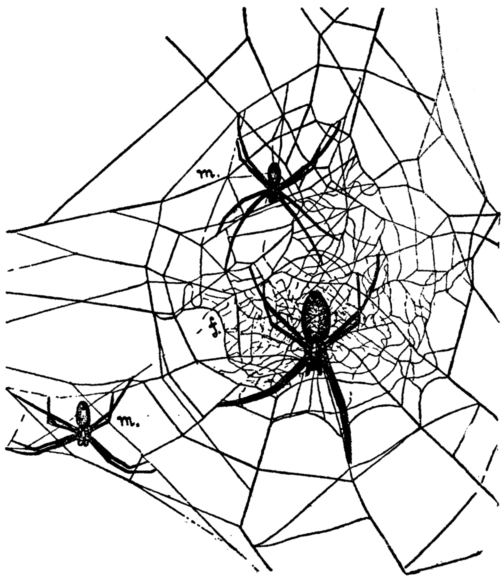

FIG. 8.

This figure represents the third main step in the approach of the male, M., to the female, F., in the mating of *Argiope transversa* (see text). It may also represent the end of the first step.

splitting horizontally is very well shown in Fig. 11 below. In one case the moulting and copulation was all done in four hours. In another, the female was beginning to moult in the morning at eight A. M., copulation began at 5.45 P. M., and the male was caught and wrapped by the female at 7.07 P. M. During the latter part of the moulting while the female's legs were about half out of the old skin, the male was constantly following the progress of the moulting. The moment she freed herself from the old skin he took the position shown in the accompanying drawing. She hung suspended by the wide strand of web which had exuded from the spinnerets while she was moulting and which is clearly shown as attached to the old moult, her legs all hanging limp. After a time she supported herself by taking hold of the threads of the side-guard of her web. After one hour and twenty-two minutes of copulation she suddenly brushed the male off and wrapped him as she would any other prey leaving him attached to the strand to which she had been hanging. She then took her position head down in the centre of her web. See Fig. 12, which shows the sequel of many acts of mating with the *Argiope*. The next morning conditions were unchanged except that she had cut

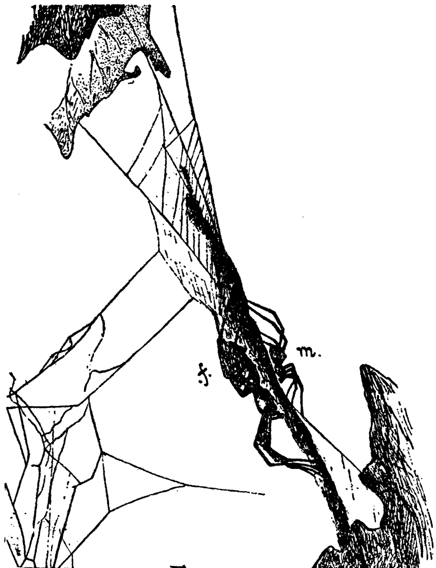

FIG. 9.

This figure shows the second step in the approach of the male toward the female in *Argiope riparia*. Any of these figures illustrating the mating of one of these two species illustrate that of the other as well.

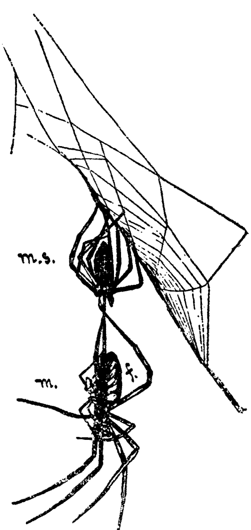

FIG. 10.

This figure represents the copulation of *Argiope riparia*. The female, F., has just dropped from the moulted skin, m. s.; m. is the male.

out the moulted skin which had lodged in the lower part of the web with the wrapped male still suspended from it.

While I believe the above process often happens, the death of the male is not always the sequel, nor does he always succeed in taking advantage of the female's moulting to secure the necessary position for copulation. In another case the female had moulted and yet the male made many attempts to approach her. At times she seemed passive, but at others she was hostile and drove him away. At night, when observations were discontinued, he rested with one fore foot on one of her hind feet. The following morning she had disappeared leaving him alive on the web. In this case the male failed to take advantage of the female's helplessness, immediately following moulting, or she failed to entrap him after coition was accomplished, and he continued in his attempts for repeated copulation. When I placed him on the sticky part of another web he was immediately caught and wrapped. (In another case I atoned for this act by freeing a male who had stuck to the web of *riparia*. He lost two legs in the accident.) The males must keep free from the adhesive spirals if they would be safe.

What must have been a similar case was observed in *A. transversa*. The male had gone through the same steps as for *riparia*. He was present at the moulting and may have succeeded in the act of coition for a few seconds during the moulting, but following this he did not again succeed in copulating although he made every effort to do so. Most of his efforts were confined to the dorsal side of the abdomen on the opposite side from the reproductive organs of the female. His palpi were repeatedly thrust into the skin of her back, or posterior part of the ventral side. The drawing below shows him in the act of doing this. After continuing his unsuccessful attempts for two hours, during the latter part of which he rested often, he seemed to give up altogether. The female was small and this was probably not her final moult. She was hostile whenever he shook the web. This made me curious to know if the female would ever be other than hostile if the male shook the web. Of course, while she is helpless through moulting it would make no difference. My observations point to the fact that the male not finding the female ready to moult leaves to return another day; also to his mating with more than a single female. It is quite possible that the moulting of the female is in part a response to the appearance of the male. Two hours later in the first case described above the female had cut out the moulted skin and the males were gone. One week later she was found dead in her web with her abdomen twisted over to one side. Whether the male in his attempted coition caused her death cannot certainly be known. Her manner of death is the only one of the kind I have observed.

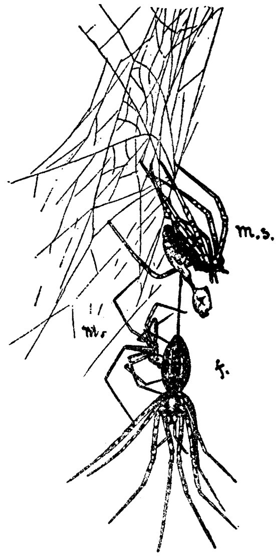

FIG. 11.

Fig. 11 represents an attempted copulation in *Argiope transversa*. The female has just moulted as in the preceding figure. The preceding steps in the two cases were much the same.

That nature has taken as careful precautions to insure the fertilization of the female spider as she has the queen bee and ant, though probably not in such a prodigal way, is proved by the fact that often there are two, or more, and sometimes even five, males on the web with one female. Fig. 8 shows but two of the three males which were present.

The above cases, which are the only complete examples of approach and copulation I have seen, prove that *riparia* and *transversa* are very similar here as in other respects. But with both I have followed the approach of the male for days only to find after a few hours' absence the moulted skin of the female and the wrapped male. In several cases the approach of the male was the same as in the completed acts observed. It is, at any rate, clear that the interpretation which McCook gave to his and Emerton's findings, which are represented in Fig. 12, is not the only one. Such do not always mean that the male has been too urgent in his attention to the female.

Let us return to our general questions. In the first place, it would seem improbable that the male is lead by sight in searching out the female. The distances are without doubt too great for his poor vision. Is it something akin to the antennal sense in ants and bees, of which Forel (25) and Miss

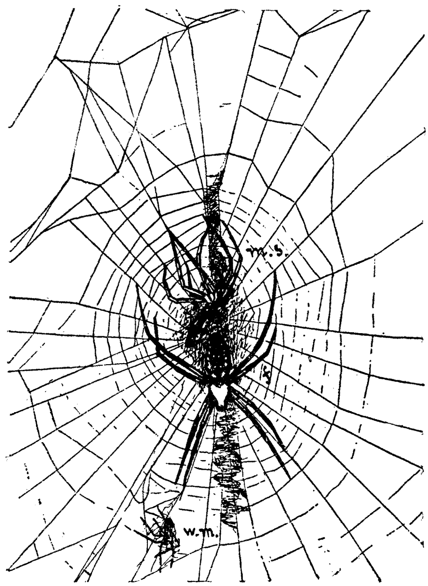

FIG. 12.

Fig. 12 shows the sequel to Fig. 10. After the female has sufficiently recovered from moulting, she wraps the male as shown in the lower part of the drawing and takes her usual position on the web.

Fielde (22) have given such good accounts? Judging from the few observations I have made, this seems improbable. A male of *A. transversa* who had conformed ostensibly to all the regular rules in paying his respects to the female, finally lost her, probably because both "feigned" and dropped to the ground at my approach. She came up about six inches distant from the old web and moulted without his presence. An hour or two later he began to wander about and his curve of search so far as I plotted it, seemed to be a wholly aimless one. It very much resembles those given by the Peckhams (41, p. 400) for spiders in search for their cocoons.

Again I found a male of *A. transversa*, with the third leg gone from the left side, on a web of *E. trifolium*. The next day he was suitor, No. 2, to a female of *A. transversa* some three feet away. Hence, it would seem quite certain that McCook's surmise that male spiders at times make mistakes is an actual fact. It also seems quite probable that males of *A. transversa* and *riparia* should make mistakes of the kind just mentioned since they are so closely allied and similar in habits. These examples rather point to the fact that male spiders find the webs of the female at random. Further progress might well be due to tactual and visual stimuli.

After he has located the female, what are the reasons for his fear of the female and his caution in approaching her? We have seen in the above account that he does manifest both caution and fear, and the typical approach in spiders would seem to be by a series of acts almost as formal as is to be found in the best human society. In the first place all solitary spiders instinctively separate from each other as soon as they leave the cocoon. The female spiders which I have placed on another's web, seem to be in great haste to get off. Can it be that the male has some of this instinctive fear of the female's web? Yet this fear and caution must give way at the right time to the sexual impulses which, of course, must be strong, in order that the male accomplish the one thing whereunto he is sent. The male must reach a high state of excitement before coition takes place. This, of course, is necessary to insure the best results of coition. Montgomery (38, pp. 135 and 142), to whose excellent article I owe much, holds that mating in spiders is more remarkable than in other animals because the male must charge, and perhaps recharge, the palpi with sperm. Lastly, the male must learn that the female is not hostile. This, in the spiders here considered, is indicated to him by her remaining quiet.

In the above statements do we find any support for believing that there is a choice by the female of the most beautiful or active males? The males on one web, Fig. 8, did fight for supremacy. In the case described above where the male did not succeed in copulating the two males on the side had an encounter. The one farthest away, or the one I had previously selected as the smallest, retreated. The victor, or second in size, then approached the largest one which happened at the moment to be resting. But the aggressor suddenly beat a hasty retreat, leaving the largest male to continue his attentions. The males of these species do not go through the antics or "showing-off" acts which are found in other species. They, however, do struggle for supremacy, and Montgomery (38, p. 144) very probably is right when he says that the female chooses that male which "first and most surely announces by his movements that he is a male." The largest and therefore earliest to develop, as I was able to select beforehand in the above example, would naturally do this.

Can we account for all the facts by natural instinct, pure and simple, or must intelligent adaptation on the part of the individual spider be appealed to? Given a physiological change in the male spider which is not without its analogy in the instinctive actions of other animals, for example, in the migration of birds and salmon, he begins his search for the female. Once on the web, at the edge or on the side screen, he next

goes to the upper edge and then down to within about one inch of her, then on opposite side. If she feels for him at any time he retreats. Next he goes to the same side, and just about now the moulting, if it is going to take place, should be indicated by her flexed legs and body farther out from the web than is usual. If she moults, the male constantly follows the progress of this act. At once when her legs drop from the moult he is in position and coition begins. Montgomery (38, p. 135) has shown that this may last hours or seconds and may be repeated many times depending on the species. He has also (p. 125) emphasized the variation to be observed in some of his species. While the series of acts constituting mating must allow for some variation, the acts of both sexes, when conditions are favorable, appear to be, in the two species here considered, pretty definitely correlated with each other. Intelligent adaptation, to any great extent, is perhaps uncalled for in their explanation.

Tropisms versus Plasticity in Instinct.

Are there any reactions in spiders which may be denominated tropisms? Almost from the very first I have been on the lookout for such reactions. For the present I have concluded that there are, at least, a few such which are unvarying enough to be classed under this head,—namely, that of standing in the web with head down, the way the *Epeirae* stand in the nest, their thygmotactic reaction to sides of the nest, the direction in which the guide lines or temporary spirals, and the outer permanent sticky spirals are put in. Figs. 1, and 8-12 inclusive, illustrate the first of these reactions; Figs. 4 and 5, the second. Standing in the centre of the web with head down is also true of the males of *Argiope*. The spiders that have nests hold approximately this same position much of the time. When they stand in the middle of the web they orient themselves in exactly the same way as the *Argiope*. It is true that in taking this position all are facing the lower part of the web, which, since it constitutes the larger half, allows them more readily to locate and wrap their prey. But we must suppose that gravity is one of the forces toward which they are reacting. This is always the same. Spiders also orient themselves unmistakably with reference to the centre of the web, both in the original construction of it and in the use of it later. Directions within the web are all the same when once the centre has been located. Indeed, if we enumerate the conditions to which spiders must adapt themselves, gravity and direction are the only ones which at once appeal to us as being constant. Yet it is evident that there are relatively few tropisms in spiders. It is surprising and almost incomprehensible how long we have

held to the belief in the non-variableness of instincts. They must of necessity vary if the individual is to use them in living successfully in an environment that in many ways is one thing to-day and quite another to-morrow.

Do the many variations pointed out above prove that the spiders here concerned have intelligence? Not conclusively it seems to me. A few of the acts observed which are similar to those noticed by Dahl do point that way. But many of the variations fall under one or the other of the very suggestive classifications of Wagner (67) which are quoted with approval by Rainbow. These are first "deviations of instinct," and, second, "variations of instinct." The first are slight and have no value in the struggle for existence. The second are greater variations from the instinctive procedure of the species. They may be seized upon by evolution and affect the future development of the species. There are many examples of these in spiders. Such as the omission of the zigzag, or the "darning" of the centre, the putting in of more outer spirals above than below the centre, *E. trifolium*, *strix*, and *sclopetaria* standing in the centre of the web instead of the nest, the different methods of treating prey, etc.

To emphasize further the place which plasticity should hold in our scheme of explanation of animal activities it is only necessary to refer to Prof. Forel's recent publications (24, pp. 562 and 563). He writes in substance as follows: In our study of insect psychology we must avoid two evils, (1) that of identifying our mind with that of the animal, and (2) of imagining that with our present knowledge we are able to construct the insect mind. On the contrary we must recognize that this insect mind and the senses, which when functioning awaken it, are derived from the primitive life of protoplasm. This life, so far as it is characterized by irritability of the nervous system and connected with a contractile muscular system, manifests itself in two ways. First, as automatic or instinctive activity and, secondly, as plastic or intelligent activity. The former is more or less adapted to the circumstances of the specialized life of a variety, species, or genus. It is insidiously analogous to the action of a machine. But nearly all the recent work in Animal Psychology clearly shows that those very animals from the reactions of which the adherents of the theory that animals are "reflex machines," get their best examples, are, in reality, able to modify their actions, use a method of "trial and error," and do have plasticity.

Any attempt to divide activities into Reflex, Instinctive and Voluntary does as much injustice to real life in the animal series (as it is hoped the many observations and facts of spider life given above will help to prove), as it does to divide

the human mind according to the old faculty psychology. This seems to me doubly true of the higher invertebrates such as the ant, bee, wasp, and spider. Weismann (70a, p. 162) says, "A sharp line of distinction between either Reflexes and Instincts, or between the latter and voluntary acts, is not to be made. They shade over into each other and this is quite equivalent to saying that in plyletic development transitions from one form of activity to another have occurred." If the above is true it follows that a "deviation or variation of instinct" may very well offer a basis for the development of intelligence.

As Miss Washburn (69) has already pointed out, Professor Royce, in his "Outlines of Psychology," has done inestimable service to Psychology by the manner in which he has made the results of Animal Psychology contribute both to the view point and manner of treatment of his subject matter. His use of the Tropisms is peculiarly suggestive. He says (56, pp. 142-143) "The researches of Loeb and others have called attention, in the recent literature of genetic psychology, to the vast importance which is possessed, in all grades of animal life, by the types of reaction which have been called the tropism of Orientation. We earlier made mention of such reactions when we were speaking of the various tropisms which Loeb has experimentally examined, as they exist in lower organisms. The general character of such reactions is that they determine, in an organism of a given type, a certain characteristic normal position of the organism with reference to its environment, and certain equally characteristic tendencies on the part of the organism to recover its normal position when it is for any reason temporarily lost, and to assume, in the presence of stimuli of certain types, certain directions of movement and certain attitudes which may persist through a great variety of special activities. The phenomena here in question are, in a sense, very familiar to us all. The animal laid upon its back may struggle back again to the normal position. Or again, the human being when engaged in normal activities either sits or stands erect. When the eyes are engaged in their normal activity, the head is held erect, or, if these normal attitudes are modified, as in reading or in writing, the modification occurs only within certain limits. To attempt to carry on the same activities when lying on one's back, leads to discomfort, and interferes with the normal special movement of the eyes. It is thus a familiar fact that a certain orientation of body, that is, a certain general direction of the organism with reference to the most important kinds of stimulation which are falling upon it, is a condition prior to all special activities. Hence the reactions of orientation are amongst the most fundamental

phenomena of healthy life. Profound disturbances of orientation necessarily imply very considerable defects and in most cases very gravely important defects, in central functions. Thus our responses to our environment are not only special deeds, such as grasping this object, or looking at that object, but include general attitudes, namely, such acts as sitting or standing erect or holding the head up in order that we may see. And the special acts are always superposed upon the general acts, in such wise that if the general tropisms of orientation are seriously disturbed, the special acts, however habitual, will be interfered with or will prove to be impossible."

Further on in the discussion of Active Attention (pp. 329-330) the same author says, "In brief, whoever is persistently attentive is expressing an attitude of the organism which has the essential character of the now frequently mentioned 'tropisms' of the animals of Loeb's experiments."

As will be evident from what has been said above of "tropisms" in spiders, this creature furnishes us with an excellent example of the fundamental tropisms of orientation and also of direction. While in a few cases these are like the tropisms in many other animal forms, they are more adaptive. The spider is capable of carrying on other and special activities without exact orientation, though it is true that she would feel more at home if normally oriented. Professor Royce's view that the "tropisms" are the basis of Attention, even of Active Attention, seems to me possible only on the assumption that instinctive activities suffer variations such as may be seized upon by natural selection. It is hoped that the present paper will help to show that the life of spiders furnishes us with some proofs of this.

SUMMARY.

1. The spiders whose names are given on page 314 show wide variation in color markings and degree of development. They also show great variation in selecting a place for a web and, for those that build one, the nest and the choice of material for the same.

2. In making the web they seem to be able to adapt themselves to the peculiarities of the place or supports for the web. They may make unusually strong any part of the web if external conditions require it. A change by the spider to a very different place has led to the greatest variation.

3. The webs vary from the normal slant, the upper outer spirals may be more numerous than the lower ones, which in a way is equivalent to turning the web upside down. Those that put in a zigzag or "winding stair" may in many cases put in only the lower half of it, or omit it altogether and the centre

may be left undarned. When a spider has the same branched twig in which to sling her web, she gives to almost each new web a different slant.

4. As for the number of parts it will be readily seen from the tables that these vary within limits. The variation among members of the same species as the "mean variation" shows is too great to be the product of an instinct followed with mathematical precision. In the case of successive webs of the same individual the same variation is found. The results obtained for the group cannot be due, therefore, to differences between individuals only. Since all of the Orb-weavers have the same sorts of changes in conditions to meet it is to be expected that their variations would be of the same kind and degree. Such is actually the case—*Argiope transversa*, *Epeira trifolium*, and *Epeira sclopetaria* showing a striking agreement in both specific and individual variation. The counts for individual *Epeira strix*, *Epeira patagiata*, *Argiope riparia*, and *Epeira corticaria* show the same thing.

5. The young spiders, especially of *E. sclopetaria*, have been watched spinning their webs and some of these have been counted. They probably choose the site for their web in the same way as the old. They certainly make the web as rapidly and they are really more perfect since the webs are so small that a large enough niche can be easily found and the weight of the spider does not bend the threads so that they stick together. I have also seen webs of the young of *A. riparia*. They are as perfect as those of the old, if not more so. Young of *E. angulata* have been seen spinning the web and they were as adept as the old.

6. The feeding habits of spiders show powers of modification that seem to be intelligent. Dahl's experiments, as also those of the Peckhams, point to the fact that spiders are able to profit by experience, and have a memory lasting a few hours. Such of my tests and observations as would prove this for the spiders here dealt with are inconclusive. *E. strix*, *E. sclopetaria*, and *A. transversa* use different methods with different prey. *A. riparia* refused after a first trial to wrap what is not food and later ignored its presence in the web.

7. The time of spinning of the web depends on the species. It is very probable that *A. transversa*, *A. riparia* and *E. trifolium* spin their webs at the first appearance of light in the morning. Old *E. sclopetaria* and *E. angulata* spin at nightfall. Young of both the latter spin at almost any time of day. *E. sclopetaria* move about at early dawn and may spin then if they have not spun the evening before. The reaction to light here is a pretty definite one.

8. The web-shaking instinct is most marked in the *Argiope*.

In fact, only one case approaching the slow rhythmic swings which they give to the web has been observed in the other species and that in *E. sclopetaria*. It is brought about by touching or otherwise disturbing the spider.

9. Tests with these spiders in a state of rest and after they have been made to shake the web, or have otherwise been put on the alert, show that they have a range of distinct vision, at least six to eight times that of clear vision under ordinary circumstances, which is about two centimeters. It may be more for very large and light colored objects.

10. The approach of the male in the mating of the *Argiope* is probably divided into a number of fairly definite steps. The male seems to hunt at random until he finds the web of the female. He then approaches her from the upper edge of the web on the same side. Next he approaches on the opposite side of the web and remains just opposite to her for some time. He then returns to her side of the web and takes his place immediately above her. If she moults he keeps close watch of her progress. As soon as she drops from the old skin, coition occurs. This may last a variable time after which the male is wrapped and dies. If the female is hostile and not ready to moult the male may leave the web. The above steps are not invariable.

12. The variations which are recorded in the foregoing sections are convincing proof that instinctive activities in spiders are variable, and it is easy to find teleological reasons for such variability. These variations are so marked in some cases that they may well be seized upon by natural selection and made starting points in the development of new types of habit, if not of new species. That they furnish a basis for intelligent behavior in these spiders is probable, though the extent to which this sort of behavior has been actually developed can be affirmed only after further study. This point and others the writer hopes to follow in later researches.

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